34. The Nestling Feathers of the Mallard, with Observations on the Composition, Origin, and History of Feathers.

By J. Cossar Ewart, M.D., F.R.S., F.Z.S., Regius Professor of Natural History, University of Edinburgh.

[Received March 7, 1921; Read March 22, 1921.]

(Plates I.–X.; Text-figures 1–14.)

I. The Nestling Feathers of the Mallard (*Anas boscas*).

In a recent paper in 'The Ibis' it is pointed out that "there is no branch of ornithology that has remained so long neglected as the study of nestling birds, nor is there one in which so many problems await solution" (1). That the study of nestling feathers has been neglected will be admitted when it is mentioned that up to 1906 it was not realized that the true feathers (pennæ) may be preceded by two generations of nestling feathers (prepennæ), that ornithologists have not yet made up their minds whether the familiar coat worn by newly-hatched chicks and ducklings corresponds to the first (protoptile) or to the second (mesoptile) nestling coat of Penguins, and that morphologists have not yet ascertained whether nestling and other feathers originally consisted of one shaft or of two complete shafts like the nestling and adult feathers of the Emu.

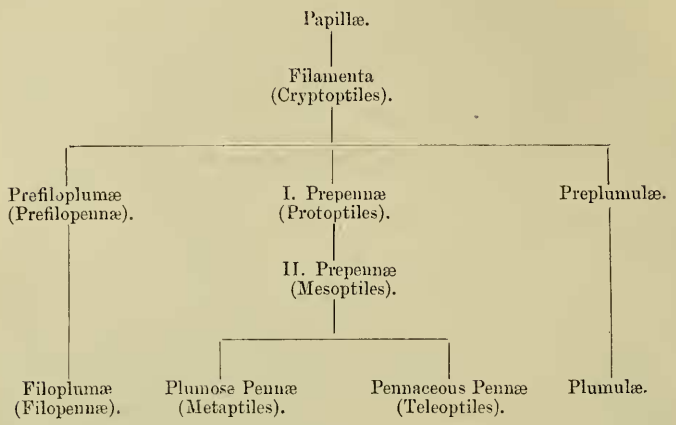
True or definitive feathers vary greatly in size and structure; nevertheless, they may be said to belong either to a plumose (metaptile) or to a pennaceous (teleoptile) type. The plumose true feathers are characterized by barbules which may possess cilia but never have hooklets (hamuli); in pennaceous feathers some of the barbules are armed with hooklets, by means of which the barbs are "woven" into a web—in the wing-quills of flying birds we have highly specialized teleoptiles; in the plumose feather from a Mallard represented in Pl. I. fig. 1 we have an example of a simple metaptile, bearing a protoptile.

In Penguins all the true feathers are probably preceded by both protoptiles and mesoptiles (text-fig. 3), but in many birds there is only one nestling coat—the mesoptiles have either been completely suppressed or are represented by inconspicuous and barely recognizable vestiges.

In most birds there are numerous hair-like feathers associated with, and intimately related to, the true feathers. As these hair-like feathers are preceded by minute prepennæ—are, in fact, degenerate pennæ,—they might be known as filopennæ.

Further, in many birds there appear between the true or contour feathers (pennæ) true down feathers (plumulæ). In all the Ducks, Geese, and Penguins examined the plumulæ are preceded by preplumulæ.

The relation of the various kinds of feathers of mature birds to nestling feathers is indicated in the following table:—



1. *The Prepennæ.*

The most concise and authoritative statement I have come across about nestling feathers occurs in 'Newton's Dictionary of Birds.' It is there stated that neossoptiles (*i. e.* protoptiles) "are characterized by (1) a very short calamus, (2) an insignificant or ill-defined rhachis—if there be one at all, (3) the almost universal absence of cilia, (4) long and slender rami (barbs), and (5) the absence of an aftershaft except in Dromæus"; in another paragraph it is stated that the barbules (radii) of the aftershaft have no cilia (2). A more recent statement about neossoptiles is that the feathers forming the familiar coat of newly hatched ducklings and chicks are not protoptiles but mesoptiles, and hence correspond to the feathers forming the long fur-like second coat of Penguins (3).

I may at once state that in Mallard ducklings the outer nestling coat consists of typical protoptiles characterized by (1) a well-developed calamus which may contain over twenty "cones," (2) a well-developed rhachis, (3) well-developed and in some cases hook-like cilia, (4) short stiff, as well as long slender barbs, and (5) by a well-developed aftershaft, the barbules of which bear cilia.

In ducklings the protoptiles vary in size—some are over 30 mm. in length and resemble plumose (metaptile) feathers, others are under 10 mm. in length and resemble preplumulæ. But the small as well as the large protoptiles consist of a calamus, a shaft, and an aftershaft. In addition to assisting the preplumulæ, and later the plumulæ, in diminishing the flow of heat from the skin, the protoptiles, as a rule, prevent water reaching the under coat

of true down; by the pigment they contain they help to make the duckling inconspicuous.

(1) *The Wing-Quill Protoptiles.*

Though Ducks have been living under domestication for well-nigh two thousand years, their nestling feathers have apparently never been systematically examined. That no serious attempt has been made to study the nestling feathers of ducks and other Anseres, and of fowls and other Galli, is made evident by a perusal of Mr. Pycraft's important monograph on the Emperor and Adélie Penguins. In an interesting chapter on the composition and sequences of the neossoptiles, after pointing out that "the penguin must certainly be regarded as having preserved what must be looked upon as a somewhat, perhaps very, ancient succession of plumages," Mr. Pycraft states that "in the light of my recent discovery" it is clear that the "down" feathers of the Galli and Anseres "do not, as I imagined, represent a primitive type of down feather homologous with the woolly, and so presumably degenerate down of say the Alcidæ, but answer to mesoptyles. The protoptyle or first generation of feathers would seem to be wanting in these birds, but I had the good fortune to discover small tufts of down adhering to the tips of the mesoptyles of a young *Chloëphaga rubidiceps*. Thus we may assume that this first generation, since it has not yet been traced, has been lost in all the Galli, and probably all the Anseres save perhaps this species and one or two allied genera" (3).

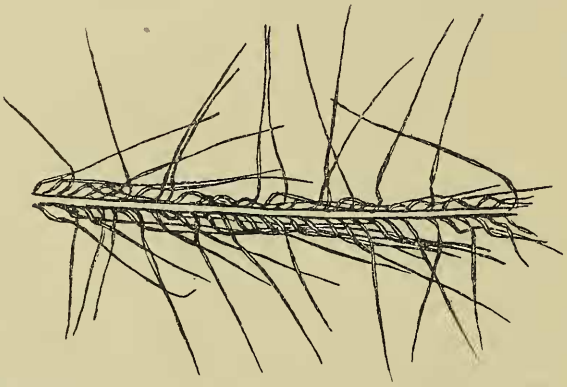
As Pl. I. figs. 2 & 3 show, I have succeeded in tracing two generations of nestling feathers in the Indian Runner Duck and in the common Domestic Goose, and thereby have proved that the coat worn by newly-hatched Ducks and Geese consists of protoptiles corresponding to the first or protoptile nestling coat of Penguins. In the case of the King Penguin the first or protoptile coat is apparently in the act of disappearing; but in all the Anseres and Galli I have examined it is the second coat that has been lost or is in the act of disappearing. Though in the wings of some Ducks and Geese well-developed mesoptiles still make their appearance, the tail-quill mesoptiles are either vestigial or have been completely suppressed. That the protoptile is in the act of disappearing in the tail of the Penguin is suggested by Pl. I. fig. 4, while Pl. II. fig. 5 clearly indicates that as the mesoptile was suppressed in the tail of the Mallard the protoptile was enlarged.

With the help of a prematurely developed "nestling tail" the Mallard duckling begins to dive at the end of the second week, but, owing to the development of the wings being retarded, flying only becomes possible at the end of the eighth week. That the development of the wing is from the outset retarded is suggested by Pl. II. fig. 6, a ten days' duck embryo. In this embryo the papillæ which develop into the tail-quill protoptiles are large,

but the wing-quill papillæ are only beginning to make their appearance*.

In a five weeks' duckling some of the tail-quills measure 50 mm., but the wing-quill rudiments at the end of the fifth week only measure 4 mm. The wing of a twenty-five days' Mallard is represented in Pl. II. fig. 7, natural size, and the protoptile of a secondary wing-quill of a thirty-eight days' Mallard in Pl. II. fig. 8. Though the wing-papillæ appear late they soon develop into filaments—filaments of a thirteen days' Mallard embryo are represented in Pl. III. fig. 9. With the exception of the calamus the development of the protoptile is, as

Text-figure 1.



Part of a barb from the shaft of a protoptile of a 16 days' duckling showing barbules spirally twisted at their origin. × 25 dia.

Text-figure 2.

Distal part of a barbule of a protoptile of a 23 days' duckling showing cilia. × 250 dia.

a rule, completed before the end of the twenty-eighth day of incubation, so that the vascular pulp—which made the development of the nestling feather possible—may be converted into bloodless pith before hatching. Even when the duckling escapes from the shell the nestling coat consists of bristle-like filaments. But as the duckling dries, the thin friable sheaths which protected the protoptiles during development disintegrate, with the result that the protoptiles expand and provide the duckling with a wonderfully complete outer nestling coat. A wing-quill

* It is conceivable that there is some relation between the slow development of the wing and the persistence of wing-quill mesoptiles.

protoptile of a twenty-six days' duck embryo artificially removed from a filament (like the long filaments in Pl. III. fig. 9) is represented in Pl. III. fig. 10.

The wing-quill protoptiles are complete feathers: *i. e.*, each consists of a calamus, a shaft, and an aftershaft. The calamus, though only 3 or 4 mm. in length, is well formed, contains several "cones," and remains intact until the protoptile is shed—in Penguins the part of the epidermic tube which represents a "calamus" usually soon splits, with the result that the individual protoptile barbs are directly continuous with mesoptile barbs (text-fig. 14). Though the growth of the shaft and aftershaft is arrested before hatching, the calamus may continue to grow after hatching.

The shaft is made up of a rhachis, continuous with the outer segment of the calamus, and usually of seven or eight pairs of barbs, which vary in length and in the number of barbules they possess. The two terminal barbs (which by uniting formed the distal part of the rhachis) end in long slender processes destitute of barbules. The aftershaft (Pl. III. fig. 11), continuous with the inner segment of the calamus, usually consists of eight barbs bearing barbules. Sometimes the four mesial barbs of the aftershafts unite to form a short rhachis. The barbules of the shaft are spirally twisted at their origin (text-fig. 1), but the aftershaft-barbules only curve slightly on leaving the barb. It has frequently been stated that aftershaft-barbules of true as well as nestling feathers have no cilia, but cilia are invariably present on the barbules of the protoptile aftershaft of Mallard ducklings. Part of a barbule with cilia is given in text-fig. 2.

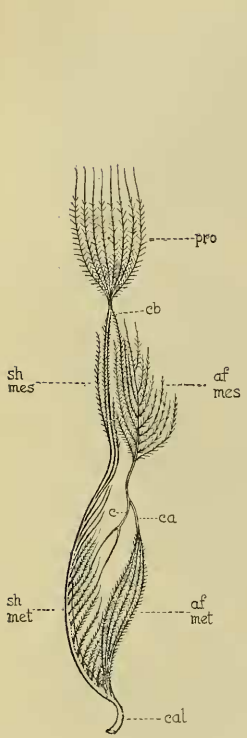
The wing-quill protoptiles may all be present at the end of the sixth week (Pl. III. fig. 12), but some of them have usually been shed before the end of the seventh week. Though Mallards begin to fly during the ninth week, the development of some of the wing-quills is only completed during the tenth week.

(2) *The Wing-Quill Mesoptiles.*

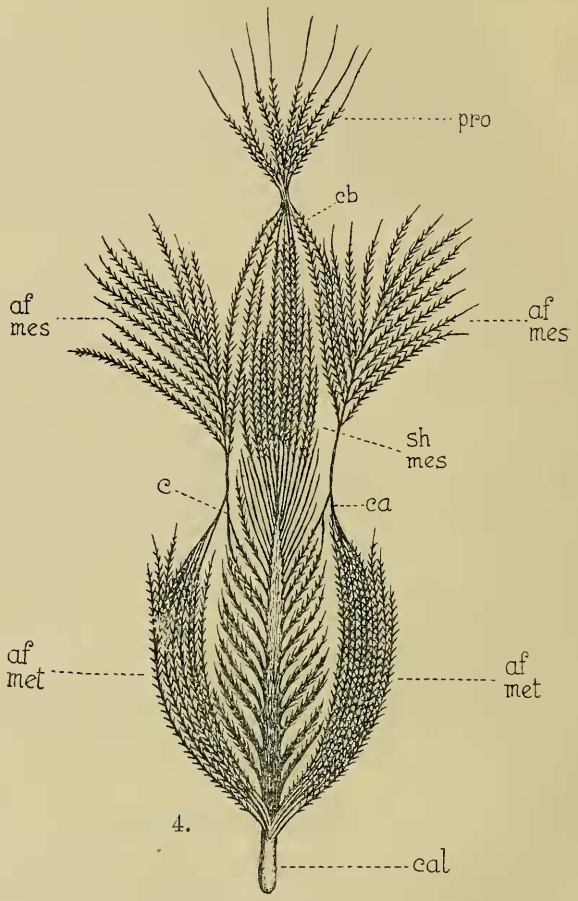
Up to 1906, as already mentioned, it had not occurred to ornithologists that true feathers (pennæ) might be preceded by two generations of nestling feathers (prepennæ), and mesoptiles have apparently not yet been recorded in connection with wing-quills.

Early in the century two National Antarctic Expeditions were fortunate enough to collect material which made possible a fairly exhaustive study of the development and history of the nestling feathers of Penguins. The penguin material brought home by the English National Antarctic Expedition was reported on by Mr. Pycraft; that collected by the Scottish National Antarctic Expedition by Dr. Eagle Clarke. In a paper published in 1906 in 'The Ibis,' Dr. Clarke announced that he had discovered two coats of nestling feathers in the Ringed and Gentoo Penguins,

Text-figures 3 & 4.



3.



4.

Diagrams indicating the relation of the mesoptile to the protoptile and to the first true feather of a Ringed Penguin:—*pro.*, the protoptile, consisting of four outer barbs representing a shaft and of four inner barbs representing an aftershaft. *sh.mes.*, shaft of mesoptile continuous distally with protoptile and proximally with the shaft of the true feather. *af.mes.*, mesoptile aftershaft also continuous with the protoptile and the true feather. *cb.*, connection with protoptile. *c.*, connection with shaft of true feather. *ca.*, connection with aftershaft of true feather. *cal.*, calamus.

and in the following year an important paper by Mr. Pycraft on the Emperor and Adélie Penguins was published which deals with the composition and sequences as well as with the structure of nestling feathers.

Dr. Clarke refrained from stating whether the silky-white protoptile coat, or the grey fur-like mesoptile coat, of the Ringed Penguin, corresponds to the nestling coat worn by newly-hatched chicks and ducklings. But Mr. Pycraft, in discussing the sequences of nestling-feathers, states that there are good reasons for assuming that in most of our common birds the first or protoptile coat has been lost, and adds that the feathers forming the adult coat of the Emu might possibly consist of mesoptiles.

Whether ornithologists have, as a rule, adopted Mr. Pycraft's views it is impossible to say, but it may be mentioned that Mr. Ingram, in the 'Ibis' paper already referred to, points out that a study of the nestling plumage of the Raptores suggests that in some cases, at any rate, it is the second and not the first generation of nestling "down" that has been suppressed (1).

When, some years ago, I was led to study the feathers of Penguins, I assumed that birds with only one nestling coat had lost the first or protoptile coat; but the examination of a number of nestlings soon made it evident that when in the Galli and Anseres there is only one generation of nestling feathers, it is owing, not to the absence of the protoptiles, but to the suppression of the mesoptiles.

In the account of the nestling feathers of the Emperor Penguin, Pycraft states that the mesoptiles are umbelliform, and that in the Adélie Penguin the mesoptile is in part attached to the main shaft, but mainly to the aftershaft. I have not had an opportunity of studying the nestling feathers of either the Emperor or Adélie Penguins, but from material placed at my disposal by Dr. Eagle Clarke I have worked out the structure of the mesoptiles of the Ringed Penguin. In this species the mesoptile is extremely complex: it consists (1) of an outer small series of barbs, which extends between the protoptile and the tip of the true feather, and hence occupies the position of, and doubtless represents, a shaft; and (2) of an inner series of barbs (text-fig. 3), arranged to form two or three bundles, which as obviously represent an aftershaft. The chief connections of the mesoptile in the Ringed Penguin are diagrammatically represented in text-fig. 4, which indicates that the mesoptile consists of a simple shaft extending between the protoptile and the tip of the true feather, and a complex aftershaft connected with the shaft as well as with the aftershaft of the true feather.

In a Mallard duckling at the end of the fifth week the mesoptile looks as if it would develop into a simple umbel not unlike the umbelliform protoptiles of Penguins. But this appearance is due to the fact that nestling feathers, like true feathers, are developed, not out of a scale-like plate, but out of an epidermic tube surrounding a highly-vascular dermic pulp and

Text-figure 5.

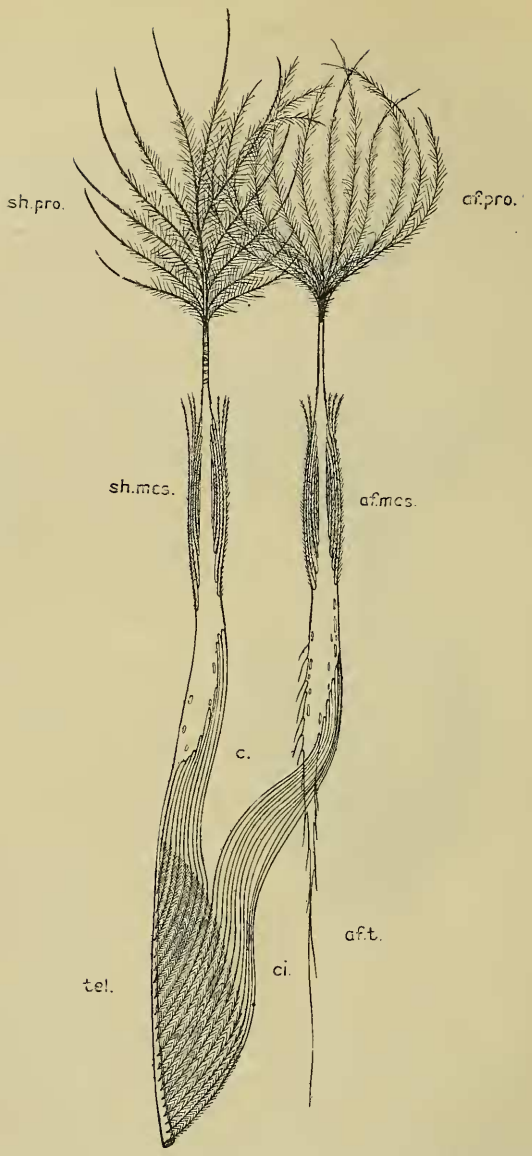


Diagram indicating the structure and relationships of the mesoptile with the protoptile and with the true feather in the Chinese Goose. The mesoptile shaft (*sh.mes.*), which lies between the protoptile shaft (*sh.pro.*) and the tip of a true feather, consists of numerous barbs and of a band representing a rhachis. Continuous with the rhachis is a perforated band from which slender cords (*c.*) proceed to the barbs forming the tip of the true feather (*tel.*). The mesoptile aftershaft is also continuous with a perforated band which ends in a vestige of an aftershaft of the true feather (*af.t.*). From the perforated band slender cords (*c* 1) proceed to barbs near the tip of the true feather. It will be observed that the aftershaft of the protoptile consists of twelve well-developed barbs armed with numerous barbules.

protected by a thin epidermic sheath. When the development is carried further, it becomes evident that in the Mallard the mesoptile consists of two sets of fibres, an outer set representing a shaft, and an inner, an aftershaft, each provided with a more or less distinct rhachis. Though the mesoptiles in Ducks may reach a considerable size, it is easier to make out their development and structure in Geese. The wing-quill mesoptiles, though well-developed in the Mallard, are not present in the Emden goose but as Pl. I. fig. 3 shows, the major wing-covert mesoptiles may reach a considerable size in Geese.

To start with, the mesoptile of a Chinese gosling looks as if it possessed a calamus (Pl. IV. fig. 13); the mesoptile barbs seem to proceed from a tube lying immediately in front of the tip of the true feather. That this tubular part represents a calamus is supported by the fact that it contains several "cones," but against the view that it is a true calamus is the fact that it is in the act of splitting longitudinally into numerous slender cords. In mesoptiles from older goslings part of the tubular portion is represented by two perforated bands, from which proceed numerous slender cords towards the wing-covert. Sometimes the mesoptile in goslings splits into two portions (Pl. IV. fig. 14, & text-fig. 5), an outer (the shaft) extending between the shaft of the protoptile and the tip of the wing-quill, and an inner (the aftershaft) extending between the protoptile aftershaft and the vestigial aftershaft of the wing-quill.

It may be mentioned that in the Anseres the mesoptiles vary greatly in structure—the proximal part of the aftershaft may be perforated and assume the form of a section of a relatively large tube (Pl. IV. fig. 14), or, like the rhachis of the shaft, be represented by a simple narrow band. Though in the Mallard and Chinese goslings the aftershaft, as well as the shaft of the mesoptile, has usually a distinct rhachis, in Emden goslings the whole of the mesoptile, as Pl. I. fig. 3 suggests, usually consists of simple barbs, one or two of which are continuous with the rhachis of the wing-covert shaft, while two or more end in a vestigial aftershaft. The barbules of the mesoptile, like those of the protoptile aftershaft, are narrow and provided with well-developed cilia. In the Ringed Penguin the mesoptiles closely agree in structure, but in the Ducks and Geese examined no two mesoptiles were alike in structure. The mesoptile coat is probably as useful now to Penguin chicks hatched within or near the Antarctic Circle as it was when originally acquired, during perhaps a cold phase of a glacial epoch. In the Anseres, though the protoptile coat still plays an important part, the mesoptile coat probably no longer counts in the struggle for existence. If this is the case there is no difficulty in accounting for its being well-developed in some parts but entirely absent in others, and for the marked variation amongst the mesoptiles which still persist.

The Mallard has wing-covert, as well as wing-quill, mesoptiles. The mesoptiles which precede the wing-coverts in the Mallard

are especially interesting, because they indicate how the suppression of the mesoptiles was gradually accomplished. In the case of the disappearing protoptiles of the King Penguin (Pl. I. fig. 4) the size is gradually reduced until they are smaller than the minute bunch of barbs which precede the filoplumes of ducklings. In the case of the vanishing mesoptiles two sets of factors are evidently at work; one set arrests the development of the mesoptile barbs, another set accelerates the development of the barbs of the true feather, with the result that in course of time the tip of the true feather is found projecting into the base of the protoptile calamus.

Though in most cases the mesoptiles are gradually reduced in size, in some cases the length is maintained and either a few barbs with barbules are developed, or the simple epidermic tube splits into two or more bands, which for a time connect the protoptile to the tip of the true feather.

It may be mentioned that though all the wing-quill protoptiles and mesoptiles may be present in the Mallard duckling at the end of the sixth week (Pl. III. fig. 12), some of the mesoptiles are usually shed before the end of the seventh week, and all are usually lost before the middle of the eighth week. But though the wing-quills lose all their nestling feathers during the eighth week, some of the feathers of the humeral track may retain protoptiles and mesoptiles to the end of the eleventh week. The existence of the wing-quill mesoptiles in the Mallard proves conclusively that the nestling coat worn by newly-hatched Ducks and Geese corresponds, not as Pycraft suggested to the second generation of prepennæ in Penguins, but to the first or protoptile generation.

(3) *The Tail-Quill Protoptiles.*

The tail varies greatly in young aquatic birds. In Penguins the tail protoptiles have almost disappeared and the mesoptiles are only represented by a few simple barbs (Pl. I. fig. 4). In the Mallard the mesoptiles of sixteen of the eighteen tail-quills have completely disappeared, but the protoptiles of all the eighteen quills are larger and more complex than in the plumose (metaptile) feather represented in Pl. I. fig. 1. In Penguins steps are soon taken to develop the tail-quills with a view to their forming with the hind limbs a tripod useful in maintaining the erect attitude. In the Mallard the protoptiles form a "nestling tail" which plays an important part during the earlier portion of the period that Mallard ducklings behave like diving ducks*.

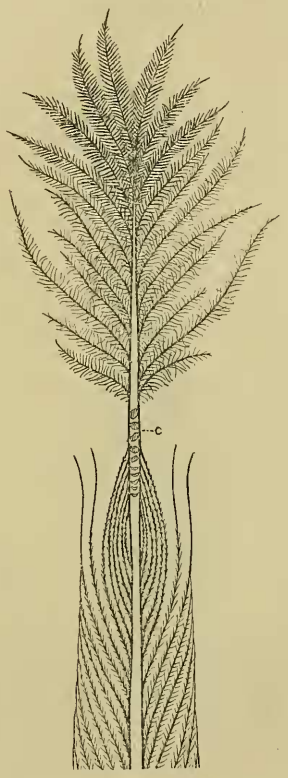
In a ten days' duck embryo the tail-quill papillæ † are easily

* The adult Mallard, Mr. G. J. Millais informs me, "hardly ever dives except when in play during the love chase, or to escape when wounded."

† There are twenty tail-quill papillæ, but only eighteen of them develop into feathers large enough to rank as tail-quills. A paper "On the development of the Feathers of the Duck during the Incubation Period" was recently communicated to the Royal Society of Edinburgh by Augusta Lamont, B.Sc.

identified (Pl. II. fig. 6), and by the twenty-fifth day of incubation they have grown into long filaments out of which escape immediately after hatching highly specialized protoptiles. During the first week the nestling tail consists only of protoptiles (Pl. IV. fig. 15), but during the second week the protoptiles are pushed from the skin by the tail-quills, or by vestigial mesoptiles. At

Text-figure 6.

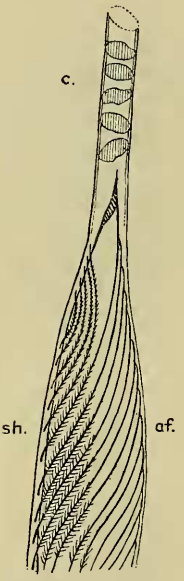


This drawing shows that the rhachis of the shaft of a typical tail-quill protoptile ends in a calamus containing "cones," that this calamus is directly continuous with the expanded distal portion of the tail-quill rhachis, and that the connection of the protoptile with the teleoptile is strengthened by barbs at the tip of the tail-quill ending in the proximal portion of the protoptile calamus.

the end of the fourth week the tail-quills may be nearly an inch in length, and they are still longer at the middle of the fifth week (Pl. IV. fig. 16). During the latter part of the fifth week the protoptiles begin to break off, and with the exception of the ninth from the middle line at each side, they are usually all shed by the middle of the sixth week.

The calamus of the protoptiles is strong and rigid and firmly fixed to the expanded tip of the tail-quill rhachis. By way of strengthening the connection between the protoptile and the tail-quill, four or more pairs of the terminal barbs of the tail-quill are attached to the protoptile calamus (text-fig. 6). At the end of the second week the "nestling" tail and the other structures concerned are sufficiently developed to admit of young Mallards

Text-figure 7.



The proximal portion of the calamus of a tail-quill protoptile containing "cones." As the calamus approaches the tip of the tail-quill it splits into an outer portion continuous with the expanded rhachis of the quill and a more slender inner portion continuous with a vestigial tail-quill aftershaft. *c.*, protoptile calamus with "cones." *sh.*, tail-quill shaft. *af.*, vestige of tail-quill aftershaft.

obtaining the greater part of their food by diving*. Notwithstanding the loss of the protoptiles during the sixth week, young Mallards usually continue to behave like diving ducks up to the end of the eighth week. From what has been said it is evident that the "nestling tail" of the Mallard duckling is not from first to last entirely composed of nestling feathers. It is a true nestling tail up to the middle of the second week, but from the

* Two of nine Mallard ducklings I had under observation began to dive on the thirteenth day: they were all diving on the fourteenth day.

beginning of the third to the end of the fifth week the true tail-quills take an ever increasing part in forming the "nestling tail." Hence nestling feathers only function during three of the six weeks that Mallard ducklings feed and disport themselves like diving ducks. When the protoptiles are shed, the tail-quills, owing to the rhachis being short and incomplete, look unfinished. Perhaps for this reason the first set of tail-quills is ere long superseded by larger and more perfect quills in which the rhachis, as in adult ducks, ends in a fine point. Usually the first set of tail-quills begins to drop out during the fourteenth week, and a new tail consisting of feathers of the adult type is eventually developed.

The Structure of the Tail Protoptiles.—The calamus of the tail-quill, like that of the wing-quill, protoptile, continues to grow after hatching. In the case of the protoptiles at each side of the middle line the calamus only reaches a length of 4 or 5 mm. and may have only three or four "cones"; but the calamus of the outer tail protoptiles may eventually measure 15 mm. and contain over twenty "cones." I expected the entire protoptile calamus to be directly continuous with the expanded tip of the tail-quill rhachis, but I found that, as text-fig. 7 shows, the calamus splits into an outer segment continuous with the tail-quill rhachis and an inner segment continuous with the rhachis of a vestigial aftershaft, the presence of this unexpected vestige of an aftershaft indicates that even the highly specialized tail quills originally consisted of two shafts, and hence were constructed on the same plan as the double feathers of the Emu.

The shaft of the tail-quill protoptiles of a Mallard duckling as a rule consists of fourteen or more pairs of barbs, each provided with barbules. As already mentioned, the majority of the barbs of the wing-quill protoptiles are long and pointed and have only a limited number of slender barbules (Pl. II. fig. 8), but some of the barbs of the tail-quill protoptiles are ribbon-shaped (text-fig. 9), and they all have barbules along their whole length. The majority of the barbules have simple cilia along both margins; but the six or seven pairs of ribbon-shaped barbules at the tip of the protoptile have large curved cilia along one margin, which differ but little from the hooklets on the barbules forming the tip of the true tail-quills. The difference between the specialized barbules with hook-like cilia at the tip of the protoptile and the slender proximal barbules with small cilia will be evident if text-fig. 8 is compared with text-fig. 9. When the broad barbules with hook-like cilia on one edge cross each other the approximation to a true teleoptile is especially marked. What Mallard ducklings gain by having the tips of the tail-quill protoptiles highly specialized is not very obvious. The aftershaft of the Mallard's tail quill consists of eight long barbs (Plate III. fig. 11) bearing slender almost straight barbules, each with two rows of small cilia.

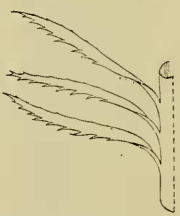
It may be mentioned that in the case of the goslings of Chinese

and Emden geese the tail-quill protoptiles—though possessing a long, strong calamus firmly connected with the rhachis of the tail-quill, a well-developed shaft, and an aftershaft made up of twelve barbs—are not provided with broad distal barbules armed with hook-like cilia. In goslings, as in ducklings, the inner segment of the calamus of the tail-quill protoptile is continuous with the rhachis of a vestigial tail-quill aftershaft.

Text-figure 8.

Two of the proximal barbules of a tail-quill protoptile; they are narrow and armed with small cilia. × 64.

Text-figure 9.



Three of the broad distal tail-quill barbules armed along one edge with tooth-like cilia (*hamuli*) of true feathers. × 64. The difference between the simple proximal and the specialized distal barbules is also indicated in text-fig. 6.

(4) *The Tail-Quill Mesoptiles.*

In sixteen of the tail-quill protoptiles of the Mallard the mesoptiles are completely suppressed, but in the remaining two—the ninth from the middle line at each side—the mesoptile is represented by a simple tube from 10 to 12 mm. in length extending between the protoptile calamus and the tip of the tail-quill. This tube, though complete to start with, sooner or later splits into two or more bands, the outer of which is continuous with the rhachis of the tail-quill, while the inner ends in the rhachis of a vestigial tail-quill aftershaft. As these bands have no barbules they evidently do not represent barbs. Though there are only vestiges of two tail-quill mesoptiles in the Mallard, there are sometimes vestiges of all the mesoptiles in cross-bred

domestic ducks. In cross-bred, as in Mallard ducklings, the feathers at each side of the true tail-quills approach in structure the wing-quill mesoptiles. In Eider ducklings the wing-quill, as well as the tail-quill, mesoptiles are either absent or represented by minute vestiges, hence the Eider supports the view that in the Anseres the mesoptiles no longer count in the struggle for existence.

(5) *The Prepennæ of the Trunk.*

About the prepennæ which precede the feathers of the head, neck, trunk, and hind limbs, very little need be said. In many cases the protoptiles closely resemble, and may be as large as, the wing-quill protoptiles, but they are sometimes so small and poorly developed that it is difficult to distinguish them from preplumulæ. The protoptile from the dorsal track of a thirty-eight days' Mallard duckling represented in Pl. I. fig. 1 is only half the size of the wing-quill protoptile in Pl. II. fig. 8; but some of the protoptiles of the wing-coverts are smaller than the majority of the preplumulæ. Usually the protoptiles of the trunk are shed about the same time as the wing-quill protoptiles, but in a small chequered area at each side of the body near the tail well-developed protoptiles are still present at the end of the eleventh week. Though mesoptiles precede some of the trunk pennæ, they are never as well developed as the wing-quill mesoptiles.

The examination of the mesoptiles of ducks and penguins lends support to the view that the mesoptile coat was specially acquired to meet a marked change of climate—a change perhaps from cold dry to cold damp conditions—and that in most cases as the climate improved the fur-like second coat was more or less completely suppressed, and a new coat, made up of feathers constructed on the protoptile rather than the mesoptile plan, was subsequently evolved. It is conceivable that some of our modern birds, *e.g.*, the Emu and Cassowary, are descended from ancestors which never acquired a mesoptile plumage.

2. *The Preplumulæ and Plumulæ.*

(1) *The Preplumulæ.*

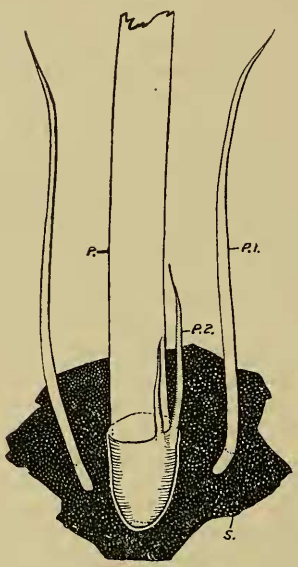
In many birds the nestling coat sooner or later consists of preplumulæ as well as prepennæ. In the Gannet the preplumulæ appear before the prepennæ, and grow so rapidly that even when the prepennæ are well developed they are difficult to find; but in the Mallard in most regions the preplumulæ are hidden by a relatively dense coat of protoptiles. Though the preplumulæ papillæ in the Mallard appear three or four days later than the protoptile papillæ, the majority of the preplumulæ are ready to escape from their filaments as soon as the duckling is hatched.

The relative size of the protoptile and preplumulæ filaments of the Mallard is indicated in Pl. III. fig. 9 and in text-fig. 10. The difference in size of the protoptiles, preplumulæ, and prefiloplumæ

is made evident by Pl. V. fig. 17, which shows a protoptile, three plumulæ, each with a preplumula on its tip, and, on the left of the protoptile, a prefilopluma on the tip of a developing filoplume.

The preplumula consists of a short conical calamus, a shaft often consisting of a short rhachis and four barbs, and an after-shaft also as a rule consisting of four barbs. It is sometimes difficult to distinguish the small protoptiles which precede small true feathers from preplumulæ, but when in ducklings the

Text-figure 10.



Filaments from a Mallard embryo.
P, proximal part of a protoptile filament. *P*.1, a preplumula filament. *P*.2, a prefiloplume filament. *S*., skin.

barbules are characterized by nodular swellings and very few cilia it may be safely assumed that the nestling feather under examination is a preplumula.

(2) *The Plumulæ.*

At the beginning of the Jurassic Age the coat of birds may have consisted only of protoptiles and preplumulæ; but in many recent birds the plumulæ form a very important part of the nestling plumage. From Pl. V. fig. 17 it may be inferred that during the fifth week the plumulæ form an inner coat as effective in preventing a loss of heat as the woolly under coat of wild sheep.

Like plumose or metaptile feathers, the plumulæ vary in size, colour, and structure, but they, as a rule, consist of a calamus, a shaft, and an aftershaft. The calamus, especially well developed in the Eider Duck, is barrel-shaped and contains relatively large cones. As it leaves the skin it divides into two portions, an outer which forms the short rhachis of the shaft, and an inner which forms the still shorter rhachis of the aftershaft (Pl. V. fig. 18). The shaft consists of a dozen or more pairs of very long slender barbs from which spring numerous slender barbules, the proximal portions of which are characterized by pyramidal swellings, while the distal portions like the preplumulæ have nodular swellings. The aftershaft (Pl. V. fig. 18) is always well developed, and like the shaft is largely made up of long barbules having the characteristic pyramidal swellings. When a plumula is shed the tip of the sheath of the growing new plumula is often found attached to the calamus. Evidence of this we have in Pl. V. fig. 19.

(3) *Prefiloplumæ and Filoplumæ.*

Nitzsch, in his account of filoplumæ, says they are strikingly distinguished from the other three kinds of feathers (contour, down, and semiplume feathers) by their peculiar position, their extraordinary slenderness, and by the entire deficiency or very small size of their vane; but he states subsequently that he believes the narrow white downy feathers of the Cormorant must be regarded as filoplumes, even though they are furnished with perfect vanes. Nitzsch further mentions that filoplumes are "associated with the contour feathers, one or even two filoplumes standing quite close to every contour feather of the head, neck, and trunk, apparently issuing almost out of the same pouch of the skin." Filoplumes are usually regarded as degenerate feathers because during development they have barbs arranged after the fashion of a down (plumula) feather.

In the Mallard during development there are usually two or more minute filaments at each side of the filaments containing the wing-quill protoptiles. These minute filaments contain prefiloplumæ. In text-fig. 10 the two short filaments (P. 2) lying in contact with the large protoptile filament are prefiloplume filaments.

In the newly-hatched duckling the minute prefiloplumæ and the large wing-quill protoptiles escape simultaneously from their sheaths—being barely visible to the naked eye, the prefiloplumæ have apparently hitherto escaped the notice of ornithologists. In course of time, as the protoptiles are pushed from the skin by mesoptiles, the prefiloplumæ are pushed from the skin by filoplumæ. The wing-quill protoptile of a thirty-eight days' duckling represented in Pl. II. fig. 8 is attached to a developing mesoptile. At the base of the mesoptile are three young filoplumes, two of which support prefiloplumes—a young filoplume with a prefiloplume attached to its tip is also seen in Pl. V. fig. 17.

Notwithstanding their small size, the prefiloplumæ have the structure of prepennæ. They are hence not dwarfed preplumulæ, as their name suggests, but dwarfed protoptiles. It is important to note that, though several developing filoplumæ may be intimately related to a protoptile, they are not imbedded in its sheath; each projects from a separate pit in the skin. At the end of the seventh week, when the filoplumes have reached a length of about 20 mm., they are still found in contact with the developing true feather. A filoplume from a forty-eight days' duckling, still carrying the minute prefiloplume on its tip, is represented in Pl. V. fig. 20. At this stage the filoplume still consists of a calamus, a shaft and an aftershaft; but as the duckling increases in size the filoplumæ in connection with the wing-quills degenerate. Each loses its prefiloplume, its aftershaft, and most of the barbs of its shaft, with the result that, as a rule, only the rhachis of the shaft and two or three vestigial terminal barbs are left.

That the filoplumes are degenerate pennæ is supported by a study of the foot-feathers of the Barn Owl (*Strix flammea*). In a newly-hatched Barn Owl one large and two small filaments are seen projecting from under the foot-scales. Soon a well developed protoptile escapes from the large mesial filament and a minute protoptile from each of the two small filaments. In course of time a simple plumose feather (metaptile), with a large aftershaft, but with a rhachis which suggests a filoplume, succeeds the large protoptile, and typical hair-like filoplumes succeed the small protoptiles.

If further proof were needed in support of the view that filoplumes are degenerate pennæ, it is obtained by the examination of the white neck feathers which form part of the nuptial plumage of Cormorants, *i. e.*, the feathers Nitzsch assumed were filoplumes. Instead of regarding the narrow neck feathers of Cormorants as filoplumes, it would be better to regard them as true feathers (metaptiles) which have undergone degeneration.

It may be added that, notwithstanding the small size of the prefiloplumæ, a microscopic examination clearly proves that they are more intimately related to protoptiles than to preplumulæ. Seeing that the filoplumes are degenerate pennæ, it might be better if the name filopenna were substituted for filopluma.

II. The Composition of Feathers.

The feathers forming the coat of the adult Emu consist of a calamus and two blades, an outer, the shaft, and an inner, generally known as the aftershaft; the wing- and tail-quills of ducks consist of a calamus and a well-developed shaft, but there is only a minute vestige of an aftershaft. Hitherto it has been taken for granted that a feather with only a vestige of an aftershaft is more primitive than a feather with an aftershaft as long and as complex as the shaft, that, in fact, the aftershaft is not a

primitive but a secondarily acquired feature. The chief reasons given for regarding the aftershaft as an accessory and secondarily acquired structure are: (1) that the aftershaft is developed from a forward elongation of the calamus, and (2) that the tip of the aftershaft of the new feather is never attached to the calamus of the feather about to be shed—that, for example, in the Emu the tip of the aftershaft of the feather of the second generation is from first to last free.

If I succeed in showing that the aftershaft, like the shaft, grows from apex to base and is completed before the calamus is formed and that, during development, the tip of the aftershaft is connected with the calamus of the feather about to be shed—is, in other words, for a time attached to the old feather—it may be safely assumed that the aftershaft is a primitive feature, and that a complete true feather (penna) like a down feather (plumula) consists of two shafts or blades.

Owen evidently assumed that a true feather was made up of a calamus and a single shaft, for he states that "besides the parts which constitute the perfect feather there is an appendage attached to the upper umbilicus called the accessory plume" (4). According to Nitzsch, the aftershaft "originates from the underside of the umbiliciform pit" (5). Gadow, in discussing the aftershaft, states that when present it is developed as "a ventral elongation of the calamus," and points out that if we consider the various types of nestling feathers "with reference to the presence or absence of an aftershaft in the Teleoptiles, we are led to conclude that this appendage and consequently also the double feathers of certain Ratitæ are secondarily acquired not primitive features" (6).

That the aftershaft is a primary feature was suggested in 1903 by Degen in a paper on Ecdysis. In the chapter on "Adventitious Plumage," Degen writes: "I may mention here that owing to the yet more primitive conditions of the feathers of the trunk in some Ratitæ, the extreme tips of the aftershafts, which in the Cassowary and the Emu attain a length equal to that of their main shafts, *jointly support the new-growth feather* with the latter" (7). But Degen, following Gadow, seems to adopt the view that the calamus is concerned with the formation of the aftershaft, for he assumes that while the one half of the calamus "deposits *substantia rhachidis externa* for the main shaft, the other half deposits" the same substance required in the building up of the other shaft! Obviously the best way to throw light on the status of the aftershaft is to study its development.

1. *The Development of the Aftershaft of Plumulæ.*—In the Mallard a preplumula consists of a small conical calamus, a shaft usually made up of four barbs, two of which coalesce to form a short rhachis, and of an aftershaft also made up of four barbs. Soon after hatching the preplumulæ are pushed from the skin by plumulæ. Some of the plumulæ at the end of the fifth week, though still bearing preplumulæ on their tips, are 15 mm. in

length and consist of two distinct bundles of barbs—a large outer bundle in a line with the shaft of the preplumula and a smaller bundle in a line with the aftershaft.

In the plumula from a five weeks' duckling represented in Pl. VI. fig. 21, the outer bundle already consists of a rhachis and eight pairs of barbs, but the inner or aftershaft bundle only consists of five pairs of barbs. By the end of the sixth week the development of both the shaft and aftershaft is complete, and the unsplit portion of the epidermic tube is giving rise to a calamus. In the completed plumula (Pl. V. fig. 18) the shaft consists of a rhachis and over twenty pairs of barbs; and the aftershaft of a rhachis with about a dozen pairs of barbs.

From Pl. VI. fig. 21 it is evident that the aftershaft of a plumula in its development and structure agrees with the shaft; as it is developed before the calamus it cannot be regarded as a secondarily acquired appendage produced from a forward elongation of the calamus.

2. *The Development of the Aftershaft of Emu Feathers.*—It has hitherto been often assumed that in the Emu the protoptile has "no distinct aftershaft." That there is an aftershaft in the first, as well as in the second and third Emu feathers, is indicated by the diagram, text-fig. 11. In the young Emus I have examined the protoptile aftershaft has, with rare exceptions, consisted of seven or more barbs longer than, or at least as long as, the barbs of the shaft. In the Emu protoptile given in Pl. VI. fig. 22, the aftershaft has a short rhachis. It is especially noteworthy that in the Emu the rhachis of the protoptile shaft, instead of ending in a hollow calamus containing "cones," is connected with the relatively thick rhachis of the shaft of the feather of the second generation by a solid band (Pl. VI. fig. 23).

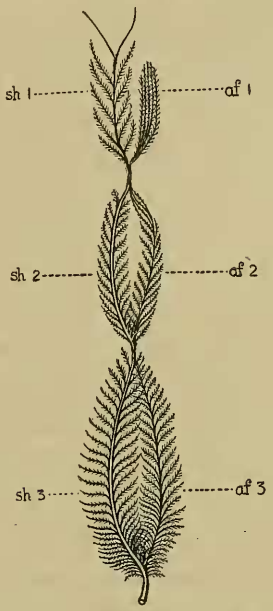
In a like manner the rhachis of the protoptile aftershaft is connected with the aftershaft rhachis of the second feather. When, as sometimes happens, the connecting bands occupying the position of a calamus separate from each other (Pl. VI. fig. 23), it becomes obvious that the tip of the aftershaft of the second feather is not free as generally assumed, but from the outset continuous with the protoptile aftershaft.

Though as in plumulæ the rhachis of the aftershaft is formed by the fusion of two barbs, the distal portion of the rhachis of the shaft is simply a continuation of the band proceeding backwards from the protoptile shaft. That the aftershaft of the feathers of the second generation is not "developed as a ventral elongation of the calamus," but develops from apex to base like the shaft, is made clear by Pls. VI. and VII. figs. 23, 24, & 25, which show the second feather at various stages of growth.

As the destined length of the second-generation feather is reached the rhachis of the shaft expands, gives off six or more pairs of relatively long barbs, and thereafter becomes continuous with the rhachis of the shaft of the feather of the third generation (Pl. VII. fig. 26). In a like manner the proximal end of the

rhachis of the aftershaft, after giving off several pairs of barbs but without appreciably increasing in width, becomes continuous with the rhachis of the aftershaft of the feather of the third generation (Pl. VII. fig. 26). When (as was the case in the specimen represented in Pl. VII. fig. 27) the two connecting bands naturally separate from each other, it is impossible to escape

Text-figure 11.



In this diagram the structure and relations of the feathers forming the first three generations in the Emu are indicated. *sh.* 1, shaft, and *af.* 1, aftershaft of protoptile. *sh.* 2, shaft, and *af.* 2, aftershaft of a feather of the second generation. *sh.* 3, shaft, and *af.* 3, aftershaft of a feather of the third generation. The aftershaft of the protoptile is from the outset free, but the tip of the aftershaft of the feather of the second generation is, to start with, continuous with the protoptile aftershaft, and the aftershaft of the feather of the third generation is also for a time continuous with the aftershaft of the second generation feather—according to Gadow the tip of the aftershaft of the second generation feather is a forward prolongation from the calamus which is never during development connected by its tip with the "calamus" of the protoptile or first generation feather.

from the conclusion that, just as the aftershaft of the second feather of the Emu is connected at the outset with the protoptile, the aftershaft of the feather of the third generation is connected with the feather of the second generation.

The feathers represented in Pl. VII. figs. 26 & 27 (from a seven

months' Emu bred in the Gardens of the Zoological Society of London) prove conclusively that in the Emu the aftershaft in origin and structure agrees with the shaft, while the feathers represented in Pl. VII. figs. 24 & 25 (from a much younger Emu in the Museum of the Philosophical and Literary Institute, Leeds) as clearly indicate that as the aftershaft is developed before the calamus it cannot be an outgrowth from the calamus. The first three generations of the feathers of an Emu are diagrammatically represented in text-fig. 11.

Before dealing with the aftershaft in the Carinatæ, attention may be directed to the remarkable Emu feather of the second generation represented in Pl. VIII. fig. 28. In this growing feather the aftershaft, instead of resembling the shaft, simply consists of two barbs bearing barbules. An Emu feather with an aftershaft represented by two simple barbs is interesting, because in true feathers near the oil-gland of ducks two long barbs sometimes occupy the position of an aftershaft. That the two long barbs in this Emu feather represent a phase in the degeneration of the aftershaft is suggested by Pl. VIII. fig. 29, a developing true feather with the protoptile intact from the rump of an eighteen days' Mallard duckling. Connected with the protoptile calamus are two bundles of barbs—a large bundle with a distinct rhachis which is obviously a developing shaft and a smaller bundle representing an aftershaft. The smaller or aftershaft bundle is connected to the inner aspect of the protoptile calamus, as in the Emu feather, by two long barbs. In course of time the large bundle in Pl. VIII. fig. 29 would have developed into a shaft like the one represented in Pl. I. fig. 1, and the small bundle into an aftershaft with a short rhachis. Possibly long barbs which represent an aftershaft will be met with in the feathers of other Ratitæ.

The two long barbs in the Emu feather in Pl. VIII. fig. 28 support the view that the coat of the adult Emu consists of true feathers and not, as Pycraft suggested, of mesoptiles.

3. *The Development of the Aftershaft of the True Feathers of Penguins.*—In the Ringed Penguin the protoptiles though umbelliform may be said to consist of two sets of barbs—an outer representing a shaft and an inner occupying the position of an aftershaft. Though in ducks and geese there is a well-developed protoptile calamus containing "cones," in penguins as in the Emu a true protoptile calamus is never developed. Soon after the protoptile escapes from its sheath the part of the epidermic tube representing a calamus splits into slender cords, which connect the barbs of the protoptile with barbs of the developing mesoptile. The mesoptile consists of a shaft made up of seven or more simple barbs which end in the tip of the true feather, and of a complex aftershaft connected with the aftershaft of the true feather. In text-figs. 3 & 4 the mesoptile aftershaft is connected to the aftershaft of the true feather by a narrow band formed by the fusion of the distal portions of the barbs of the

aftershaft of the true feather. Pycraft considered the "ribbon-shaped stem" connecting the mesoptile to the aftershaft of the true feathers as somewhat remarkable, because "in all other instances yet known the nestling-down when attached to contour feathers is attached to the rami (barbs) of the main shaft" (9). When it is realised that in Penguins the mesoptile may have a well-developed aftershaft the connection of the mesoptile with the aftershaft of the true feathers ceases te be remarkable. Though in the Ringed Penguin the mesoptile aftershaft is decidedly larger and more complex than the shaft, it is developed at the same time as the shaft, and is directly continuous with the aftershaft of the true feathers. That in Penguins the aftershaft of the true feathers has the same origin as the shaft is made abundantly evident when the development of the feathers of the fourth generation is studied. In Pl. VIII. figs. 30 & 31 we have feathers from a moulting King Penguin in the Scottish Zoological Park. From fig. 30 it is evident the new feather has from the first been double, consisted of outer barbs representing a shaft and of inner barbs in the position of an aftershaft. Had the development proceeded the tip of the aftershaft would have been set free when the old feather was shed. In fig. 31, the shaft having been removed, the aftershaft is seen emerging from the tip of the sheath which invested the growing feather. These figures show that in Penguins the aftershaft of a feather of the fourth generation is for a time as complete as in the Emu. The aftershaft of the mesoptile and of the first true feather of a Ringed Penguin are diagrammatically represented in text-figs. 3 & 4.

4. *The Development of the Aftershaft in the Ptarmigan, the Common Fowl, and the Guillemot.*—As already mentioned, it has been suggested that in Grouse, Fowls, and other Galli the feathers forming the first nestling coat may correspond to the mesoptiles forming the second nestling coat of Penguins. Against this view it may be pointed out (1) that unlike the mesoptiles, but like the protoptiles of Penguins and Ducks, the first nestling feathers of the Galli are developed in filaments; (2) that in structure they are intermediate between the protoptiles of Penguins and Ducks; and (3) that they are sometimes succeeded by vestiges of mesoptiles. Degen mentions that in Grouse the aftershaft may be two-thirds the length of the shaft but, as Pl. IX. fig. 32 shows, the aftershaft in Grouse may be as long and as complex as the shaft—the only difference in the feather figured apart from its width is that, as in the Emu, the rhachis of the aftershaft is slightly shorter than the rhachis of the shaft. In the Ptarmigan the protoptile often consists of fifteen barbs, eight representing a shaft with a short rhachis, and seven forming an aftershaft also with a short rhachis. From the protoptile calamus there proceed about twenty barbs, which in some cases readily separate into three distinct bundles—a large one destined to form the tip of the shaft, and two small ones which later unite to form the tip of the

aftershaft. In some metaptiles the rhachis of the shaft extends to the tip of the feather, in others it ends in two slender barbs some distance from the tip. Though at the outset in Grouse both the shaft and the aftershaft of the true feather may consist of several more or less distinct bundles, sooner or later the outer barbs give rise to the shaft, while the inner form an aftershaft. When the destined number of barbs for the shaft and aftershaft have been produced the splitting of the epidermic tube is arrested, and steps are taken to form a calamus in which "cones" make their appearance. Evidently in Grouse, as in Penguins, the aftershaft is not a forward elongation of the calamus. An interesting stage in the development of a Ptarmigan true feather is given in Pl. IX. fig. 33.

It has been asserted once and again that "in the great feathers which form the 'quill' or 'flight' feathers (remiges) of the wing and the tail-quills (rectrices) the aftershaft is invariably wanting"*. Assuming that in the case of the wing-quills the aftershaft is invariably absent, it might be argued, that these all-important feathers differed in their origin and history from the other true feathers, that while the trunk feathers may possibly have developed from an epidermic tube, the wing- and tail-quills were formed by the splitting of elongated scales. Attention has already been directed to the fact that in the Mallard during the earlier stages in the development of the wing- and tail-quills, there is a vestige of the distal portion of an aftershaft (text-figs. 5 & 7). That in wing- and tail-quills there may also be a vestige of the proximal portion of an aftershaft is made evident by Pl. IX. fig. 34, which represents the aftershaft of a wing-quill from a full-grown Grouse.

Fowls are not supposed to have the aftershaft as well developed as Grouse, nevertheless, as Pl. IX. fig. 35 shows, the aftershaft in the silky breed may be as long as the shaft. In its development the aftershaft in the silky breed follows the same course as in Ptarmigan.

In the Guillemot the aftershaft is, to start with, sometimes as long as the shaft. A Guillemot feather from the side of the trunk is represented in Pl. X. figs. 36 and 37. In this case the protoptile consists of seventeen barbs. Of the seventeen barbs nine end in the tip of the shaft of the true feather, four end in barbs of the shaft which join the rhachis a considerable distance from the tip, and four, which represent the protoptile aftershaft, are connected with the aftershaft of the true feather (Pl. X. fig. 37).

Evidently the history of the aftershaft in Grouse, Fowls, and Guillemots affords no support to the view that the aftershaft is a secondarily acquired appendage, and may be said to fully establish the view that a complete true feather like a plumula consists of a calamus and two shafts.

* Pycraft, 'A History of Birds,' p. 9.

III. Origin and History of Feathers.

It seems to be generally assumed by naturalists and others interested in birds that feathers are modified scales, and were originally acquired to enable birds to fly. When evidence of the scale origin of feathers is asked for, the reply usually is, "If you accept the view that birds were evolved from Reptile-like ancestors you may safely also accept the view that feathers are specialized scales." Having adopted the view that feathers are modified scales, investigators interested in the coat of birds proceeded to inquire if each feather corresponds to an entire scale or to part of a scale. Wiedersheim favoured the view that each feather represents a complete scale, but Bornstein (13) and others came to the conclusion that a feather papilla only represents a fragment of a scale.

How scales were transformed into feathers has been indicated by various writers. Baron Frances Nopcsa, in a paper "On the Origin of Flight," states that we may quite well suppose "birds originated from bipedal long-tailed cursorial reptiles which during running oared along in the air by flapping their free anterior extremities," and added that the double running and flapping action would subsequently easily lead to an enlargement of the posterior marginal scales of the antebrachium, and eventually to their development into actual feathers (10). Lull, another believer in the transmission of acquired somatic characters, points out that the anterior extremities of birds when in the making would be more effective if their breadth was increased, and that an increase of the size of the scales along the arm margin would be a ready means to this end. Lull then proceeds to say the "scales would extend, lighten, and ultimately evolve into feathers which would not only subserve the function of flight, but acting as clothing retain and aid in the increase of temperature" (11). Similar views are held by W. K. Gregory, who tells us the Pro-Aves jumped lightly from branch to branch and finally from tree to tree partly sustained by the long scale-like feathers of the pectoral and pelvic wings.

The view that feathers are modified scales has long been held by Pycraft. In a work published in 1910 Pycraft points out that, to start with, the body clothing of birds probably consisted of relatively large scales, "those covering the hinder border of the incipient wing growing longer would still retain their original overlapping arrangement and along its hinder border would in their arrangement, appearance, and function simulate the quills of modern birds; as their length increased they became also fimbriated and more and more efficient in the work of carrying the body through space."

It is now evident that the wing-quills of birds are preceded by nestling feathers, and may be regarded as modified protoptiles: hence the question at issue is, Are the protoptiles modified scales?

It is inconceivable that the small protoptile forerunners of the wing-quills of Ducks were evolved from enlarged scales, which as they increased in length became fimbriated. The more the history of feathers is studied the more untenable becomes the belief in their origin from scales. When special attention is directed to the phases through which feathers pass during their development, it becomes evident that in an attempt to trace their origin we are not concerned with the wing-quills or other contour feathers, but with the feather papillæ, and still more with the filaments, in which the nestling feathers are developed. It is conceivable that by the appearance of new and dominant factors in the germ-plasm, scale papillæ, instead of developing into scales, developed into feather filaments, but it is difficult to imagine how scales by growing longer and splitting were transformed into double-shafted nestling feathers. There is little chance of the geological record ever throwing any light on the origin of either feather papillæ or feather filaments, hence we must make the most of the embryological record. Thus far the embryological record has afforded no support to the view that scales in whole or in part were concerned in the making of feathers.

When birds first acquired feather filaments it is impossible to say, but we may assume that when the remote ancestors of birds and mammals became warm-blooded any outgrowths from the skin which prevented a loss of heat would from the first count in the struggle for existence.

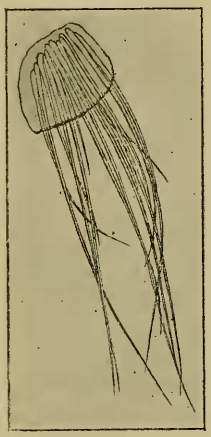
A hint as to the nature of the coat in the progenitors of mammals we have from Armadillos, and an indication of the kind of coat worn by the Pro-Aves is obtained by studying the development of nestling feathers, more especially of the protoptiles of feather-footed birds. The Six-banded Armadillo has an extensive scaly covering, but only a sparse coat of hair; birds, with few exceptions, have during development a more or less complete coat of filaments*, and probably in Owls the foot-feathers still bear the same relation to scales as in the primeval birds. In the developing Armadillo a stage is eventually reached when hairs are seen projecting from under the developing scales or from the skin between the scales. The number of hairs developed in connection with scales varies. There are often groups of three hairs projecting from under the tail scales of mammals; in the Six-banded Armadillo there are often three or four hairs to a scale, but sometimes only one; in the small Argentine Armadillo *Chlamydophorus*, as text-fig. 12 shows, fifteen hairs may be developed in connection with one foot-scale.

In Armadillos and other mammals having scales as well as hairs there is no evidence that the hairs are ever developed from scales.

* All the birds I have examined, with the exception of the House Sparrow, had a more or less complete coat of protoptiles—in the Rook a nestling coat is said to be absent, but even in Rooks there are a few well-developed nestling feathers.

That in ancient birds feathers were intimately associated with scales is suggested by the feather papillæ having approximately the same arrangement as the scales of reptiles, by feathers emerging from under scales above the tarsal joints of the Woodcock, and by chicks and ducklings having vestiges of scales in connection with the feather filaments of the legs. In the case of Grouse and other birds with only one feather emerging from under a foot-scale, we are tempted to assume that each foot-feather is developed from part of the scale it is associated with. But when we find three feathers projecting from under the foot-scales of the Barn Owl (*Strix flammea*) and seven or more feather filaments occupying an area equivalent to a foot-scale, we

Text-figure 12.



Scale from the foot of the small Argentine Armadillo (*Chlamydophorus*) from under which proceed a number of hairs developed from the skin underlying the scale. The three filaments proceeding from under the foot-scales of Barn Owl embryos like the hairs associated with the scales of mammals are developed from the skin under the scales and not by a splitting of the scales or from fragments of the scales.

are less inclined to admit that each of the foot feathers of Grouse corresponds to part of a scale. When the development of the foot feathers of the Barn Owl is studied, one large and two small filaments are found projecting from many of the scales; the large filament contains a protoptile, and each small filament contains a prefilopluma. Similar groups of filaments which occur above the tarsal joint are overlapped by scale vestiges, but in the three feather groups on the head scales are conspicuous by their absence. The well-developed scales in connection with the foot-feathers and the vestiges of scales in connection with feathers above the tarsal joints support the view that birds, to start with, had a complete scaly covering and a sparse coat of feather filaments.

As in feather-footed birds the feather papillæ are from the first as distinct from the scale papillæ as the hair rudiments are distinct from scales, there seems no escape from the conclusion that the foot feathers are not modified scales. Further, when it is realized that the foot feathers often belong to a simple primitive type, have the aftershaft as long as the shaft, and that in many birds there are seven or more feathers occupying the position of an ancestral scale, we are justified in assuming that feathers, like hairs, were originally intimately related to, but not derived from, scales.

As a matter of fact, believers in the scale origin of feathers admit that the foot feathers of recent birds are not derived from the scales from under which they project. Just as it has been assumed that the aftershaft in Emu feathers is a secondarily-acquired structure, it is assumed the scales on the feet of birds are secondary structures. That the scales overlapping the feathers of modern birds were secondarily acquired and that the foot-feathers were formed from the original foot-scales, are gratuitous assumptions wholly unsupported by facts.

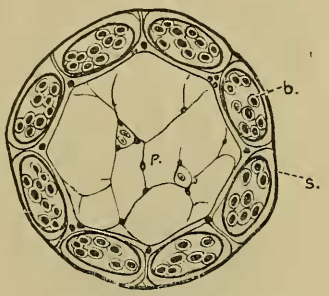
How or when feather filaments made their appearance it is impossible to say, but we may safely assume that many centuries elapsed before there was evolved in each filament a more or less complex feather; needless to say that unless a filament in which a feather was evolving was of more use than a simple filament, natural selection took no part in providing birds with their original coat of what are now familiarly known as nestling feathers. On the other hand, when one bears in mind that blood-vessels extend right to the tip of a feather filament, and not merely a short distance into its root as in a hair, it is probable that early specialization of the filaments was well-nigh inevitable. Given a constant flow of blood through the axis (pulp) of the filament, an inner epidermic layer capable of rapidly adding new cells to the middle layer, an outer epidermic layer forming a protecting sheath and, in addition, an ever increasing demand for a coat capable of arresting the flow of heat from the skin, changes were almost bound to take place in the bristle-like outgrowths projecting from under or between the scales of the remote ancestors of birds.

Judging by what takes place to-day during the development of the simple protoptiles of pigeons, the first step in the making of a feather probably consisted in the splitting of the middle epidermic layer to form hair-like barbs. The result of this splitting of the hollow cone formed from the middle epidermic layer of a pigeon filament is represented in text-fig. 13. The appearance of a completed pigeon protoptile after escaping from its protecting sheath is represented in Pl. X. fig. 38.

The protoptiles of Penguins represent a second stage in the evolution of true feathers (text-fig. 3). Like the pigeon protoptiles all the barbs are alike (form a tassel or umbel), but by sprouting they have acquired barbules.

A series of links connect the relatively simple umbelliform protoptiles of Penguins with the highly-specialized protoptiles of Ducks and Emus. There are good reasons for believing that the warm-blooded progenitors of birds and mammals were evolved out of reptile-like ancestors during a period when desert conditions prevailed. How long this period lasted, and to what extent feathers had been specialized when it came to an end it is impossible to say, but judging by what happens during the development of the wing-quills of the Mallard, it may be assumed the period of aridity came to an end, and a glacial period had fairly set in long before wing-quills and other true feathers were evolved. In other words, before protoptiles had been modified to form metaptiles and teleoptiles, progress in the evolution of true feathers was

Text-figure 13.



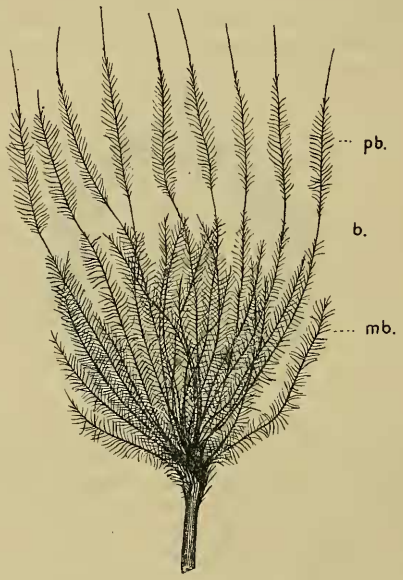
Section through the filament of a Pigeon in which the middle epidermic layer has been split longitudinally to form barbs. *s.*, the thin sheath which disintegrates immediately after hatching. *b.*, one of the eight barbs formed by the splitting of the hollow cone formed by the middle epidermic layer. *p.*, the pulp containing blood vessels, *i. e.*, the dermis or true skin which extends during development to the tip of the protoptile. After Davies.

arrested owing to the necessity of providing birds with a fur-like coat as capable of arresting the flow of heat from the skin as the dense coat now worn by Polar Bears and other Arctic mammals.

The discovery by Dr. Eagle Clarke and Mr. Pycraft of a mesoptile coat in penguins has profoundly modified our views about the plumage of birds. We do not yet know if the remote ancestors of all our modern birds acquired a mesoptile coat—probably in the case of the ancestors of the Ratitæ this was unnecessary—but the more the nestling feathers are studied the evidence of the existence of two coats of prepennæ in the ancestors of modern birds is increased. The fur-like mesoptile coat is probably as well developed to-day in penguins as it was in their remote ancestors of the Jurassic Age; relatively large mesoptiles still occur in ducks and geese, and I have found recently distinct vestiges of a mesoptile coat in pigeons. How long birds, or most

of them, in order to survive required a fur-like coat throughout life we have no means of knowing; but this much is certain, that in most recent species of birds the mesoptile coat is in the act of being suppressed, or has already disappeared—even in the King Penguin chicks it is probably never worn in the Antarctic for more than 9 or 10 months. From what we know about the mesoptile coat it seems to have been originally produced partly by lengthening the protoptiles and partly by the development of

Text-figure 14.



A developing mesoptile of an Adélie Penguin. In penguins the mesoptiles consist, as a rule, of numerous barbs which in some areas may reach a length of over three inches. A true protoptile calamus containing "cones" though present in ducks is seldom met with in other birds. As the protoptile is pushed from the skin the inner ends of the protoptile barbs, destitute of barbules, separate from each other and are subsequently seen to be continuous with mesoptile barbs. *mb.*, one of the numerous barbs of the developing mesoptile. *pb.*, one of the nine protoptile barbs, each of which is connected with a mesoptile barb. *b.*, one of the nine slender cords which together for a time played the part of a protoptile calamus.

new barbs. This is suggested by text-fig. 14, which represents a developing mesoptile feather from the breast of an Adélie Penguin. The nine barbs forming the protoptile are directly continuous with nine mesoptile barbs; the rest of the mesoptile consists of barbs having no connection with the protoptile. As Pycraft points out, the second coat of the Adélie Penguin is "a

long, dense woolly covering, so dense that it is difficult to expose the skin." In course of time the protoptile coat is shed and the mesoptile coat is pushed from the skin by the true feathers.

The long fur-like mesoptile coat of the King Penguin suggests that during the Ice Age, which succeeded the period of desiccation, the evolution of true feathers was arrested, and that the mesoptiles cannot be regarded as representing a stage in the evolution of true feathers. Though to the naked eye the mesoptile barbules seem to be identical with the barbules forming the protoptiles, they are seen to differ when examined under the microscope—instead of being nearly straight they are spirally twisted at their origin. In the case of King Penguin chicks the mesoptiles differ from the protoptiles more than in the Adélie chicks, and, as already pointed out, the mesoptiles of the Ringed Penguin decidedly differ from both the protoptiles and the metaptiles. In all the three Penguins mentioned the first true feathers differ from the prepennæ which precede them. Hence, though the prepennæ and all the true feathers which succeed them must be regarded as links in a chain, it should be borne in mind that the first link differs both in function and structure from the second, and the second from the third. Further, it should be borne in mind that there are good reasons for believing that, but for the advent of an Ice Age, the protoptiles at a comparatively early period would have been succeeded by true feathers, and that probably long before Archæopteryx made its appearance on the scene some millions of years ago, steps would have been taken in most birds to suppress the fur-like coat of mesoptiles, now apparently only well developed in Penguins.

In conclusion, it may be stated that a study of the development of birds suggests: (1) that their coat, to start with, consisted of various kinds of simple filaments; (2) that in course of time the hollow epidermic cone in each filament, in some incomprehensible way, was converted into a protoptile or preplumula: (3) that the protoptiles in some cases soon acquired the chief characteristics of true feathers; (4) that for a time progress was arrested in order to provide birds (or most of them) with a fur-like (mesoptile) coat, by way of giving them a chance of surviving during the cold phases of an Ice Age: (5) that as the climate improved the mesoptile coat was in many cases superseded by a coat of true feathers; and (6) that by the specialization of feathers along the posterior margin of the hands and forearms and the sides of the tail, birds of the Archæopteryx type were eventually evolved capable of flight, or at least of gliding easily from tree to tree.

Text-figures 1, 2, 8, 9, 12 are from drawings by Miss Augusta Lamont, B.Sc., text-figures 3–7 and 10, 11, 13, 14 are from drawings by the author, all the other figures are from photographs by Mr. John Chisholm.

Towards defraying the cost of the drawings and photographs a grant was obtained from the Moray Fund of the University of

Edinburgh and a grant has been voted from the Carnegie Trust for the Universities of Scotland, towards the cost of publishing this paper.

In addition to material in the form of ducklings, goslings &c., bred at Craigybield, Penicuik, it ought to be mentioned that valuable contributions for the study of nestling feathers were provided by the Director of the Zoological Society of Scotland, and that but for the Institution of the Scottish Zoological Park I would not have been led to undertake research work on the Structure and History of Feathers. Further, it ought to be mentioned that during the investigation I received valuable material from the Zoological Society of London, the Royal Scottish Museum, and the Philosophical and Literary Institute of Leeds, and that I am especially indebted for specimens that proved most useful to Colonel Ashley, M.P., Miss Clerk of Penicuik, William J. Gordon, Esq., of Windhouse, Yell, Shetland, Professor Meakins, the University of Edinburgh, and Professor Philip J. White, the University of North Wales.

References to Literature cited in Paper.

1. Ingram, Collingwood.—'The Ibis,' October 1920, p. 856.
2. Gadow, Hans F.—Newton's 'Dictionary of Birds,' p. 243.
3. Pycraft, W. P.—"The Emperor and Adélie Penguins," Nat. Ant. Expedition, Zoology, vol. ii. p. 12. 1907.
4. Owen, R.—Comparative Anat. vol. ii. p. 235.
5. Nitzsch.—'Pterylography,' English Translation, p. 8. 1867.
6. Gadow, Hans F.—Newton's 'Dictionary of Birds,' p. 245.
7. Degen.—Trans. Zool. Soc. vol. xvi. pp. 362 & 363.
8. Pycraft, W. P.—Trans. Zool. Soc. vol. xv. p. 164.
9. ,, ,, Nat. Ant. Expedition, Zool. vol. ii. pp. 7 & 8.
10. Nopcsa.—Proc. Zool. Soc. 1907.
11. Lull.—'Organic Evolution,' pp. 533 & 534. 1917.
12. Pycraft.—'A History of Birds,' p. 39. 1910.
13. Bornstein.—Archiv f. Naturgesch., Band I. Supplement, heft 4.

EXPLANATION OF THE PLATES.

Plate I.

Fig. 1. Protoptile and metaptile from vicinity of preen gland of a 38 days' Mallard. The mesoptile has been suppressed. The long barbs proceeding from the inner aspect of the protoptile calamus towards the calamus of the metaptile are vestiges of a metaptile aftershaft. × 2.

2. Protoptile, mesoptile, and tip of a wing-quill of a 5 weeks' Indian Runner duckling.

3. Protoptile, mesoptile, and tip of a wing-covert of a 6 weeks' Emden gosling.

4. Tip of tail-quill of a young Ringed Penguin (n. s.).

Plate II.

Fig. 5. Tail-quill and protoptile of a 5 weeks' Mallard duckling (n. s.).

6. A 10 days' Mallard embryo. The tail-quill papillæ are well developed, but there is little indication of the wing-quill papillæ.

7. Wing of a 25 days' Mallard duckling showing the wing-quill protoptiles (n. s.).

8. Wing-quill protoptile from a five weeks' Mallard duckling attached to tip of developing mesoptile.

Plate III.

Fig. 9. Filaments from a 13 days' Mallard embryo; the long filaments contain developing protoptiles, the small ones preplumulæ or prefiloplumæ. × 2.

10. Wing-quill protoptile artificially removed from a filament of a 26 days' Mallard embryo.

11. Aftershaft of the protoptile of a duckling.

12. Wing of a 38 days' Mallard duckling showing mesoptiles between the protoptiles and the developing primary and secondary wing-quills. Lying between developing wing-quills (each still invested by a sheath) are wing-coverts in which the mesoptile is vestigial.

Plate IV.

Fig. 13. Protoptile, mesoptile, and tip of wing-quill of a Chinese gosling. Though the mesoptile seems to be umbelliform and to end in a calamus, it really consists of a shaft and an aftershaft from which slender threads proceed to the tip of the true feather.

14. In this figure the proximal portion of the mesoptile is represented. It consists of a narrow, perforated band representing the rhachis of the mesoptile shaft, of a broad perforated band representing the rhachis of the aftershaft, and of numerous slender threads which connect these bands with the shaft and the vestigial aftershaft of the true feather.

15. Nestling tail of a 7 days' Mallard duckling. The protoptiles at each side of the middle line have been pushed from the skin by the developing true tail-quills.

16. The "nestling tail" at the middle of the fifth week. It now consists of growing true tail-quills as well as of protoptiles, usually with the exception of the ninth from the middle line at each side the protoptiles are directly continuous with the tail-quills—in other words, in the tail of the Mallard duckling nearly all the mesoptiles have been completely suppressed.

Plate V.

Fig. 17. Nestling feathers from the back of a 33 days' Mallard duckling. The large protoptile has a distinct calamus containing "cones." To the left of the calamus are: (1) a filoplume with a minute prefiloplume on its tip; and (2) two plumulæ each carrying a preplumula, to the right a plumula with a preplumula on its tip. × 5.

18. A plumula from a young Aylesbury duck showing a large shaft consisting of long, slender barbs springing from a relatively short rhachis and a well-developed aftershaft with a short rhachis.

19. The calamus of a naturally shed plumula with part of the sheath of the growing plumula attached.

20. A developing filoplume with a prefiloplume at its tip from a 7 weeks' Aylesbury duckling. × 2·5.

Plate VI.

Fig. 21. Developing plumula from a 5 weeks' duckling. The aftershaft is developing from apex to base in exactly the same way as the shaft. × 4.

22. A protoptile from a young Emu showing an aftershaft with a short rhachis.

23. Emu feathers of the first (protoptile) and second generation. The protoptile shaft is directly continuous with the shaft of the second feather, and the protoptile aftershaft is continuous with the aftershaft of the second feather.

Plate VII.

Figs. 24 & 25. In 24 we have an early stage in the development of an Emu feather of the second generation. In 25 the development of the second generation feather has been nearly completed. In both cases the aftershaft is developed in the same way as the shaft—the tip of the aftershaft of the second feather is continuous with the protoptile aftershaft and the tip of the shaft is continuous with the protoptile shaft.

Fig. 26. Emu feathers of the first, second, and third generations. The tip of the aftershaft of the feather of the third generation is continuous with the rhachis of the aftershaft of the feather of the second generation.

27. In this specimen the tip of the aftershaft of the second generation feather had lost its connection with the protoptile, and the tip of the aftershaft of the third generation feather had lost its connection with the "calamus" of the feather of the second generation.

Plate VIII.

Fig. 28. Emu protoptile and a developing feather of the second generation, the aftershaft of which is represented by two barbs. × 5.

29. Developing feather from rump of 18 days' Mallard duckling. This feather consists of two portions, one, the larger, representing a shaft, and one representing an aftershaft, connected like the Emu feather given in fig. 28, to the protoptile by two barbs.

30. Breast feathers from an adult moulting King Penguin. The growing feather consists of a shaft and an aftershaft connected by their tips with the calamus of the feather about to be shed.

31. In this figure the shaft of the new feather has been removed to show the connection between the developing aftershaft and the old feather.

Plate IX.

Fig. 32. Grouse feather with an aftershaft as long and as complex as the shaft.

33. A protoptile and a developing true feather from a young Ptarmigan. The part of the developing feather with a distinct rhachis represents the shaft, the part in which a rhachis has not yet appeared represents an aftershaft.

34. Calamus and aftershaft of the wing-quill of a Grouse.

35. Feather of a fowl of the Silky breed with an aftershaft as long as the shaft.

Plate X.

Figs. 36 & 37. Feather from a nestling Black Guillemot. 36, represents the shaft, and thirteen barbs of the protoptile. 37, the four remaining protoptile barbs connected with the rhachis of the aftershaft which was detached along with the calamus.

38. Protoptile of a Wood Pigeon connected to the tip of a true feather by a vestige of a mesoptile. The pulp projects from the tip of the teleoptile. Note that the barbs resemble hairs, have no barbules.